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# Self-regulatory Depletion in Dogs: Insulin Release is not Necessary for the Replenishment of Persistence

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## Abstract

It has been hypothesized that self-control is constrained by a limited energy resource that can be depleted through exertion. Once depleted, this resource can be replenished by the consumption or even the taste of glucose. For example, the need to inhibit reduces subsequent persistence at problem solving by humans and dogs, an effect that is not observed when a glucose drink (but not placebo) is administered following initial inhibition. The mechanism for replenishment by glucose is currently unknown. Energy transfer is not necessary, though insulin secretion may be involved. This possibility was investigated in the current study by having dogs exert self-control (sit-stay) and subsequently giving them (1) glucose that causes the release of insulin, (2) fructose that does not result in the release of insulin nor does it affect glucose levels (but is a carbohydrate), or (3) a calorie-free drink. Persistence measures indicated that both glucose and fructose replenished canine persistence, whereas the calorie-free drink did not. These results indicate that insulin release is probably not necessary for the replenishment that is presumed to be responsible for the increase in persistence.

(182 words)


Key words: self-regulation, persistence, depletion, persistence, canine, fructose, glucose

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## 1. Introduction

Relative to other animals, humans have remarkable self-control. Some psychologists argue that this difference exists because humans have a sense of “self”, and the ability to compare their current self with that of a standard or idealized self (Baumeister and Heatherton, 2004). Some have proposed that the desire to behave in consonance with one’s standard or ideal self is what sustains self-control (Carver and Scheier, 1998; Baumeister et al., 1998). According to self-discrepancy theory, young children and animals may not be able to override their impulsive responding because they have not yet developed a self concept (Higgins, E.T., 1987; Carver and Scheier, 2002). This perspective on human behavior reflects a belief in dualism, and although popular, it fails to account for common inhibitory processes and the neurophysiological mechanisms that maintain them. For example, Gailliot et al. (2007) has observed that human self-control is reliant on blood glucose, which is a limited physiological energy resource that can be depleted through use. Requiring participants to exert self-control (by having them control their attention while watching a video) depletes their blood glucose levels and once depleted, participants persist less in solving word puzzles and make more errors on the Stroop task. But, if participants consume a replenishing glucose drink (but not a calorie-free placebo), these performance decrements are not observed (Gailliot et al., 2007). Analogous research has reported a similar phenomenon in dogs (Miller et al., 2010). Dogs that are required to control their physical movement and sit still for 10 min (in comparison to dogs placed in a cage for the same duration)

show reduced persistence on an unsolvable puzzle task. Furthermore, a glucose (but not a sweet calorie-free) drink eliminates this effect.

According to Gailliot et al. (2007) the consumption of glucose replenishes persistence by raising blood glucose levels and providing direct energy for brain processes. Yet, a recent series of experiments by Molden et al. (2012) have challenged this metabolic hypothesis by investigating whether self-control exertion by humans reliably depletes systemic glucose levels and whether increases in blood glucose levels are necessary to observe the replenishment of persistence. Their results suggest that there are no self-regulatory induced decreases in blood glucose levels for participants who are food restricted for 4 hrs and tested in the evening with a perceptual vigilance task. Furthermore, Molden et al. (2012) observed that fasted participants, who rinsed their mouths with a sugar solution for 5 s after completing a depleting task, were replenished (as measured by increased persistence on a handgrip task and performance of the Stroop task) than participants who rinsed with a noncaloric aspartame solution. Thus, the taste of glucose was sufficient for replenishing persistence even in the absence of increases in blood glucose levels. Subsequent research by Sanders et al. (2012) replicated these results. In addition, Hagger and Chatzisarantis (2013) observed that the taste of glucose also replenished human participants and increased persistence on an unsolvable anagram task more than the taste of an aspartame placebo.

The observation that the taste of glucose is sufficient for replenishing persistence argues that energy transfer is not necessary. Thus, it has been suggested that the oral detection of glucose by taste receptors replenishes by stimulating areas of the brain that

affect motivation. The taste of glucose activates the anterior cingulated cortex (ACC) and the ventral striatum (Chambers et al., 2009), which are two regions of the brain involved in the representation of food rewards (Rolls, 2007), and are likewise involved in the motivation and regulation of goal-oriented behavior (Holroyd and Yeung, 2012; Harsay et al., 2011). Glucose also elicits the release of dopamine in the medial prefrontal cortex (Touzani et al., 2010). Accordingly, it is proposed that it is the dopaminergic activation of these regions by glucose that replenishes persistence (Chambers et al., 2009; Molden et al., 2012). This account is plausible; however, researchers have not yet eliminated alternative and perhaps complementary metabolic mechanisms.

Insulin release may be a metabolic mechanism that contributes to replenishment of persistence by glucose. The act of rinsing one's mouth with glucose has been shown to elicit a cephalic phase insulin response in humans (Goldfine et al., 1969; Yamazaki, and Sakaguchi, 1986) in contrast to aspartame (Smeets et al., 2005; Bruce et al.,1987). Given that insulin is critical for neural processes (Mielke, and Wang, 2011), and the administration of insulin to human and nonhuman animals improves cognitive abilities (Haj-ali et al., 2009; Schiöth et al., 2012), glucose induced release of insulin may contribute to replenishment. It is worth noting that cephalic phase insulin responses are elicited when taste receptors activate afferent fibers of the vagus nerve (Teff, 2011). The vagus nerve regulates autonomic functions such as heart rate and gastric function (for a review see Ruffoli et al., 2012) and it is of particular interest as it is also implicated in self-control (Thayer et al., 2009), and the depletion of persistence (Segerstrom and Nes, 2007).

The purpose of the current study was to examine whether insulin is a necessary contributor to the replenishment of persistence by glucose. To accomplish this objective, we investigated whether fructose, like glucose, would eliminate the deficits caused by initial exertion of self-control. Fructose does not directly provide energy for cellular processes, nor is it actively transported across the blood brain barrier like glucose (Simpson et al., 2007). In addition, it has little effect on blood glucose levels as it is digested primarily in the liver (Tappy and Le, 2010). The liver metabolizes fructose much like a lipid, and the energy is either converted to glucose or lactate (a process that takes hours, not minutes) or it is converted into glycogen (for a review see Sun and Empie, 2012). The stored glycogen then can be converted to glucose if necessary through glycogenolysis (Tappy and Le, 2010). Humans and dogs share this metabolic process (Shiota et al., 1998). Furthermore, the consumption of fructose does not increase insulin synthesis or secretion like glucose does, because insulin is unnecessary for metabolizing fructose by humans (Tappy et al., 1986; Tappy, and Le, 2010) and nonhuman animals (Curry, 1989).

If insulin secretion contributes to self-control replenishment, then depleted subjects should be more replenished following the consumption of glucose than fructose or a calorie-free placebo. However, if other mechanisms are involved which rely on the detection of carbohydrates, both fructose and glucose should be capable of replenishing persistence, but not a sweet calorie-free placebo.

This research was conducted with dogs using a conventional two-task paradigm (Baumeister et al., 1998). Self-control was manipulated by initially requiring dogs to sit

still alone in a room for 10-min (stay) or caging them for the same duration (cage). Dogs were then presented with an unsolvable puzzle toy and their persistence was assessed.

## 2. Methods

### *2.1. Subjects*

Dogs were selected as subjects for this study as is has been previously observed that requiring the exertion of behavioral inhibition by dogs depletes subsequent persistence, a deficit that can be eliminated by the consumption of glucose (Miller et al., 2010). Moreover, since dogs do not recognize themselves in mirrors and do not have a sense of “self” which some have theorized to be integral in human self-control (see self-discrepancy theory: Higgins, 1987), the results obtained would have general implications for the mechanism responsible for the depletion and replenishment of persistence.

We recruited 12 dogs (*Canis familiaris;* 6 males and 6 females), all privately owned by students and faculty of the Department of Psychology at the University of Kentucky. The dogs had been previously trained on command to sit and stay for at least 3 min using positive reinforcement. Owners deposited their dogs at the Canine Comparative Cognition Laboratory for further training and testing by researchers familiar to them. Three dogs were dropped from the experiment: one (female) died from an accidental injury, one (male) was dropped due to medical problems, and one (male) was dropped for behavioral reasons, leaving data from 9 dogs for analysis. The participating dogs’ ages ranged from 24 to 96 months (*M* = 52 months); all had been spayed or neutered. Of the dogs that participated in the experiment there were 4 Golden Retrievers, a Soft-Coated Wheaten Terrier, a Cavalier King Charles Spaniel, a

Boxer, and 2 dogs of mixed breeding.

*2.2. Materials and Training*

Dogs were given a Tug-A-Jug toy (available in three sizes from Premier Pet Products, Midlothian, VA). This toy consists of a clear cylinder with a hole at the end through which treats can be obtained when the cylinder is appropriately manipulated (see Figure 1). When dogs received this toy for training sessions it was half-filled with Pet Pride brand dog kibble (The Kroger Company, Cincinnati, OH) mixed with 15 ml of diced hot dog and they were allowed to play with it for 5 min daily. The dogs' interaction with the toy during training sessions was carefully monitored by a researcher and when the toy dispensed half of the available kibble-hot dog mix it was removed, refilled, and then returned to the dog for the balance of the session. The training sessions ensured that dogs did not extinguish responding to the toy during experimental sessions. In both training and experimental sessions, dogs weighing between 5 and 10 kg were given an x-small-sized toy (1 dog), those weighing between 10 and 20 kg were given a small-sized toy (2 dogs), and those weighing over 20 kg were given a medium/large toy (6 dogs). The dogs were not fed for at least 8 hours prior to the experimental sessions and all testing and training sessions occurred during the day Monday through Thursday between 9:30 am and 12:00 noon inside a white painted room (3.9 m long x 3.8 m wide).

*2.3. Procedure*

Six training sessions preceded each experimental session, and each dog participated in seven experimental sessions, the order of which was counter-balanced and randomly assigned. Experimental sessions were held about 10 days apart. Each

dog participated in seven experimental sessions, the order of which was counter-balanced and randomly assigned. Each dog was tested in both the self-control condition (sit-stay) and the cage condition under each of three treatments (glucose, fructose, and placebo). Because there was a large drop in persistence from the first test to the second test regardless of the condition, we reran the initial condition as the seventh session and dropped first session data. If the decline in persistence between the first and seventh session was greater than 50% (2 subjects) we also reran the coupled condition (stay or crate under the same treatment) as an eighth session. Data from session 2 was dropped in those two cases.

When the dog was in the self-control condition it was cued to sit and stay in the center of the room. The experimenter then exited the room while the dog maintained its position. The experimenter watched the dog (without being seen by the dog) via a small carefully placed mirror. If the dog moved from its position, the experimenter returned and recued the dog to sit and stay. Both the number of cues and the time at which each cue was given were recorded. The dog remained alone in the room for a total of 10 min (inclusive of the time needed for recuing).

When the dog was released, the experimenter gave it a small piece of hot dog (2 g) and praised it for 30 s. After 30 s, the dog was given a glucose drink (3.75 cal per kg of the dog's weight), a fructose drink (3.75 cal per kg of the dog's weight), or a sugar-free placebo drink (0 cal). The placebo drink consisted of 0.15 ml of sucralose per kg of the dog's weight. The sweetener was dissolved in water (2.46 ml per kg of the dog's weight). The beverage was administered via small Boston round bottles with Yorker dispensing caps (Consolidated Plastics, Stow, OH) by squirting it directly into the dog's

mouth. This ensured that each dog ingested the entire beverage. For the following 2 min, the experimenter sat quietly while the dog was allowed to digest the beverage. This 2-min duration was sufficient for digestion, insulin response, and for the orally administered glucose to be transported into the brain (Betz, Gilboe, Yudilevich, and Drewes, 1973; Ishida et al., 1983).

When the dog was in the cage condition, the procedure was the same as in the self-control (stay) condition except that the experimenter placed the dog inside an open wire dog cage (.9 m x .6 m x .7 m) and the door of the cage was closed. The experimenter then exited the room. The experimenter returned to the dog to recue it to get inside of the cage at the same times in the session as the dog had needed recuing in the previous stay condition. If the dog had not yet run in the stay condition, the dog was recued at 1, 3, and 7 min. The dog was released from the cage after 10 min and the experimenter gave it a small piece of hot dog (2 g) and praised it for 30 s. The procedure then continued as in the self-control condition.

After the 2 min digestion interval, the dog was tested with the persistence measure, a Tug-A-Jug toy from which the dog kibble and diced hot dog mix had been removed and replaced with items that were too large to exit the mouth of the toy: 1, 2, or 3 small woven rawhide balls (3 cm diameter, number determined by the size of the toy), a small block of wood (3.8 cm long × 2.54 cm tall × 1.9 cm wide) and a solid hot dog. The items moved freely in the toy and it is likely that the dog could see, smell, and hear these items, though it could not release them from the toy. The time that the dog persisted in playing with the toy was assessed using a stopwatch. The toy was retrieved once the dog had not made contact with it for 2 consecutive min. The timer was started

and stopped as a function of physical interaction with the toy. Thus, the total duration reflects the amount of time that the dog was actively persisting. During this time the experimenter remained quiet and did not interact with the dog. The experimenter timing the dog was blind to the treatment.

*2.3. Data analyses.*

All data were examined for distribution normality. The persistence time data was positively skewed (skewness = 2.05). Thus, the data were transformed logarithmically (Judd and McClelland, 1989), improving the distribution substantially. The transformed data were then subjected to analysis using 2 x 3 within-subjects analysis of variance (ANOVA) with self-control condition (Stay or Cage) and drink (Glucose, Fructose, or Placebo) as repeated measures. Planned comparisons between the self-control conditions as a function of drink were made using paired *t*-tests. All analyses were conducted using SPSS statistical software and a significance level of .05 was applied.

**3. Results**

The results indicated that the dogs given a placebo drink showed less persistence with the puzzle toy following the self-control manipulation than following the cage manipulation. Dogs given a glucose drink persisted in interacting with the toy whether or not they had had to exert self-control prior to the test. Dogs given a fructose drink also persisted in interacting with the toy whether or not they had had to exert self-control prior to the test. There was little difference between persistence following the glucose drink as compared to the fructose drink. The results are presented in Figure 2 plotted as Stay Persistence (s) and Cage Persistence (s) for each condition.

The 2 x 3 within-subjects analysis of variance (ANOVA) with self-control (Stay or

Cage) and drink (Glucose, Fructose, or Placebo) as variables revealed a nonsignificant effect of self-control, $F(1,8) = 3.80$, $p = .09$. The effect of drink also was not significant, $F < 1$, however, there was a significant Self-control × Drink interaction, $F(2, 16) = 8.82$, $p = .003$.

Planned comparisons indicated that among dogs given the placebo drink, those required to exert self-control persisted significantly less than those not required to exert self-control, $t(8) = 12.52$, $p = .007$. In contrast, the persistence of dogs given the glucose drink did not differ significantly between the self-control and control conditions, $t < 1$. Similarly, the persistence of dogs given the fructose drink also showed no significant difference between the self-control and control conditions, $t < 1$ (see Figure 2).

**4. Discussion**

The results obtained here further support the hypothesis that human and animal self-control share a biological commonality, arguing against accounts requiring a sense of self (Carver and Scheier, 1998). Dogs are a species that may not recognize themselves in mirrors, but they are a species capable of inhibiting behavior. And, like humans, this regulatory control is depleting and can have negative effects on subsequent persistence. The consumption of carbohydrates, in this case fructose and glucose, replenished persistence for depleted dogs, whereas a calorie-free placebo did not. The observation that fructose (a sugar that does not elicit either significant insulin secretion or increases in blood glucose) was as replenishing as glucose (a sugar that does significantly increase insulin secretion and blood glucose) suggests that the release of insulin does not play a role in the replenishment of persistence by glucose, and provides support for a centrally mediated mechanism.

Since glucose supplementation is not necessary for the replenishment of canine or human persistence (Molden et al., 2010; Sanders et al., 2012; Hagger and Chatzisarantis, 2013), and fructose can replenish persistence despite not being able to provide immediate energy to the brain, it is likely that replenishment occurs as a consequence of changes in neural transmission. Increases in dopamine release in specific brain areas may increase motivation and persistence. The taste of fructose, like glucose, increases dopamine release in the medial prefrontal cortex in rats (Malkusz et al., 2012; Touzani et al., 2010). As the dogs were tested shortly after drink consumption, our results can be explained by increases in dopamine release. However, other neurotransmitters may have also been involved. Though the taste of fructose elicits dopamine release, its digestion does not (Sclafani and Ackroff, 1994). The latter point is of interest because recent research with humans has observed that the digestion of fructose can enhance problem solving to the same degree as glucose, a sugar that does elicit dopamine release during digestion (Miller et al., 2013). The observation that fructose enhances performance to the same degree as glucose during digestion (despite differential dopaminergic activation) suggests that the activation of the vagus nerve may be involved and that replenishment may depend on the release of norepinephrine and serotonin. The afferent connections of the vagus nerve provide direct projections to many of the modulatory regions of the brain that have been implicated in executive control and motivation (Ruffoli et al., 2012) and electronic vagal nerve stimulation affects the release of norepinephrine and serotonin in rats (Dorr and Debonnel, 2006). Thus, further investigation into noradrenergic and serotonergic mechanisms is warranted and may ultimately lead to a more comprehensive

understanding of self-regulatory depletion and cognitive fatigue, the latter of which has already been strongly linked to serotonergic depletion by researchers who have studied the effects of tryptophan depletion (the amino acid precursor to serotonin) on cognitive fatigue (Mendelsohn et al., 2009).

For dogs, the present research has implications regarding alternative means of replenishment. It is not wise to administer sugary beverages to dogs for the purposes of increasing persistence on a regular basis, as the chronic consumption of sugars has been linked to long-term neurodegeneration and decreased executive function (van der Borght et al., 2011; Ross et al., 2009). Thus, it would be useful if the results obtained here motivated research on the effects of other nutrients (that similarly activate the vagus nerve) on replenishment. One promising candidate would be a lipid, rather than a carbohydrate. Medium-chain triglycerides (MCTs) are a type of saturated fat that is digested rapidly in the liver and activates the vagus nerve (Bach and Babayan, 1982), and the chronic consumption of MCTs appears to have neuroprotective effects on canine (and human) executive function (Pan et al., 2010; Reger et al., 2004). Like glucose, this energy substrate can be metabolized into a form that can be transported across the blood brain barrier (i.e., ketones). Research with diabetics has shown that MCT consumption can preserve executive function even during states of hypoglycemia (extremely low levels of blood glucose) (Page et al., 2009).

As mentioned earlier, we chose to measure the depletion of persistence on an unsolvable puzzle task. This measure is likely to be more sensitive to motivational manipulations than other tasks requiring attentional control or working memory. However, there is reason to believe that analogous results would have been obtained if

the secondary task was a search task or measured impulsivity as initial behavioral inhibition has been observed to negatively affect canine memory and impulsivity (Miller, 2010; Miller et al., 2012). Moreover, human research has reported task general effects (Molden et al., 2012, Sanders et al., 2012; Hagger and Chatzisarantis, 2013). An initial act of self-control by humans affects persistence, as it does performance of the Stroop task. Both appear to be equally sensitive to the taste and consumption of glucose.

A limitation of the present study is the small sample size. Given an a priori power calculation using the observed effect size from Miller et al. (2010), we started with a sufficient sample size. However, we lost three subjects during the execution of this project and were unable to readily replace them.

Although the conclusions we draw from this study rest on the assumption that fructose and glucose differentially affect glucose and insulin levels, there is a large body of evidence that supports this assumption (for reviews see Riby et al., 1993; Tappy and Le, 2010).

It is clear that more investigation is necessary to fully explain the mechanism of replenishment and the effects of various types of nutrients on self-control and persistence. Given the importance of these processes to the success and wellbeing of humans as well as dogs, continued investigation should be of substantial benefit to both species.

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## Author Notes

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*Figure 1.* The Tug-A-Jug toy (available in three sizes from Premier Pet Products, Midlothian, VA) that was used to measure persistence.

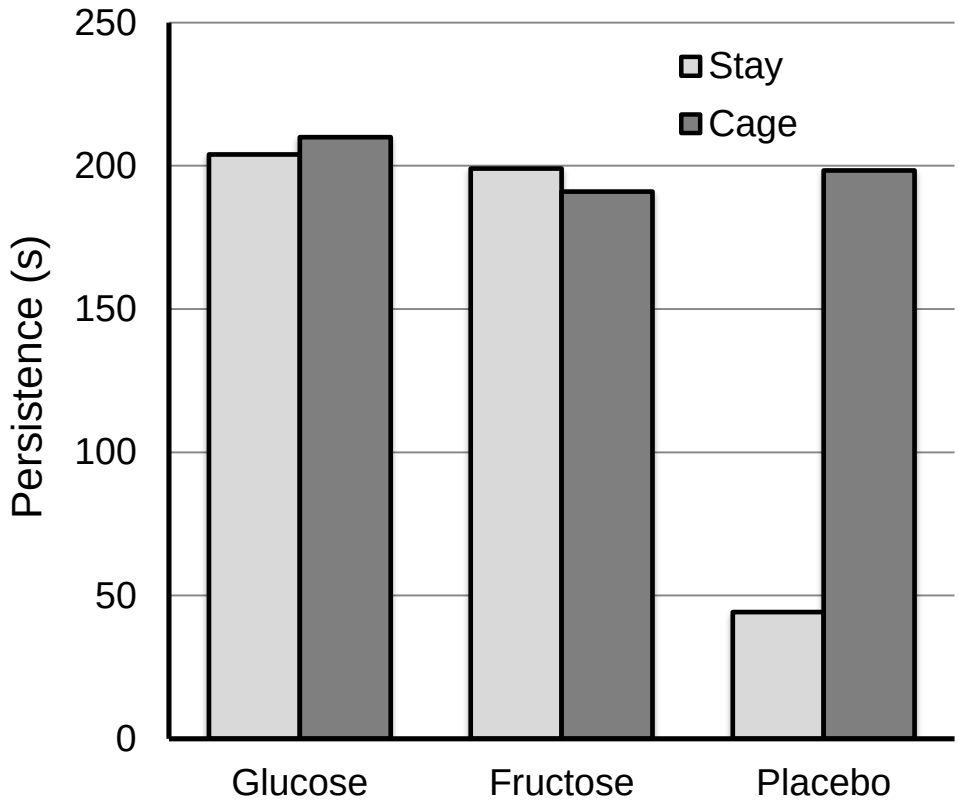


*Figure 2.* Mean persistence on the unsolvable task as a function of self-control condition (stay or cage) grouped by drink type (Glucose, Fructose, or Placebo).